Impact of anthropogenic factors on affiliative behaviors among bonnet macaques

Short Title: ***Human Impact on Affiliation in Bonnet Macaques***

Krishna N. Balasubramaniam[a] Ph.D.

Pascal R. Marty[a] Ph.D.

Małgorzata E. Arlet[b] Ph.D.

Brianne A. Beisner[a,c] Ph.D.

Stefano S. K. Kaburu[d] Ph.D.

Eliza Bliss-Moreau[c,e] Ph.D.

Ullasa Kodandaramaijah[f] Ph.D.

Brenda McCowan[a,c] Ph.D.

[a]Department of Population Health & Reproduction, School of Veterinary Medicine, University of California, Davis, Davis, California, United States;

[b]Department of Human Evolutionary Biology, Institute of Anthropology, Adam Mickiewicz University in Poznań, Poland

[c]Neuroscience and Behavior Unit, California National Primate Research Center, University of California, Davis, Davis, California, United States;

[d]Department of Biomedical Science and Physiology, Faculty of Science & Engineering, University of Wolverhampton, WV1 1LY, United Kingdom;

[e]Department of Psychology, University of California, Davis, Davis, California, United States;

[f9]IISER-TVM Centre for Research and Education in Ecology and Evolution (ICREEE), School of Biology, Indian Institute of Science Education and Research Thiruvananthapuram, Maruthamala P.O., Vithura, Thiruvananthapuram, India. 695551

Corresponding author:

Krishna N. Balasubramaniam E-mail: krishnanatarajan@ucdavis.edu

Department of Population Health & Reproduction, School of Veterinary Medicine

University of California at Davis

One Shields Avenue, Davis CA 95616 USA

Abstract:

Objectives: In primates, allogrooming and other affiliative behaviors confer many benefits and may be influenced by many socioecological factors. Of these, the impact of anthropogenic factors remain relatively understudied. Here we ask whether interactions with humans decreased macaques' affiliative behaviors by imposing time-constraints, or increased these behaviors on account of more free-/available-time due to macaques' consumption of high-energy human foods.

Materials and Methods: In Southern India, we collected data on human-macaque and macaque-macaque interactions using focal-animal sampling on two groups of semi-urban bonnet macaques for 11 months. For each macaque within each climatic season, we calculated frequencies of human-macaque interactions, rates of monitoring human activity and foraging on anthropogenic food, dominance ranks, grooming duration, number of unique grooming partners, and frequencies of other affiliative interactions.

Results: We found strong evidence for time-constraints on grooming. Macaques that monitored humans more groomed for shorter durations and groomed fewer partners, independent of their group membership, sex, dominance rank, and season. However, monitoring humans had no impact on other affiliative interactions. We found no evidence for the free-time hypothesis: foraging on anthropogenic food was unrelated to grooming and other affiliation.

Discussion: Our results are consistent with recent findings on other urban-dwelling species/populations. Macaques in such environments may be especially reliant on other forms of affiliation that are of short duration (e.g. coalitionary support, lip-smacking) and unaffected by time-constraints. We stress on the importance of evaluating human impact on inter-individual differences in primate/wildlife behavior for conservation efforts.

Key Words:

Allogrooming

Anthropogenic factors

Human-macaque interactions

Time-budgets

Bonnet macaques

Inter-individual differences

Introduction:

In humans and other group-living animals, affiliative social behaviors have many health and fitness-related benefits (Kappeler et al., 2015; Nunn et al., 2015), and are important for maintaining group social structure (Hinde, 1976; Kappeler & van Schaik, 2002). In nonhuman primates (hereafter primates), social or allogrooming (hereafter grooming) is one of the most commonly observed forms of social affiliation. In primates, grooming confers health-related benefits, such as changes in physiology related to coping with stress (Keverne et al., 1989; Shutt et al., 2007), removal of ectoparasites (Duboscq et al., 2016; Tanaka & Takefushi, 1993), and better thermoregulation (McFarland et al., 2016). Grooming also functions to establish and maintain long-term social bonds, supports group-wide social structure, increases mating opportunities, and allows access to other cooperative benefits from conspecifics such as agonistic support during conflicts (reviewed in Henzi & Barrett, 1999; McFarland, 2018). These benefits tend to outweigh the potential costs of grooming, which include decreased vigilance for predators (Cords, 2019), reduced resting or foraging time (Dunbar et al., 2009), and greater exposure to parasites (Nunn, 2012).

In primates, variation in grooming and other forms of affiliation may be influenced by ecological conditions (e.g., resource distribution and abundance, predation pressure, disease risk: Nunn, 2012; Sterck et al., 1997; Wrangham, 1980) and the social environment (e.g. group size, dominance rank, availability of close kin or mates: Chapais, 2005; Henzi & Barrett, 1999; Lehmann et al., 2007; Schino, 2001; Seyfarth, 1977). In comparison to these socioecological factors which have operated over longer evolutionary time-scales, humans and anthropogenic landscapes represent relatively recent environmental selection pressures on primate behavior. Given the globally increasing significance of human-wildlife interactions and coexistence (Barua et al., 2013; Dickman, 2010; Nyhus, 2016), and the shared ecology and evolutionary history of humans and primates (Fuentes, 2006; Fuentes & Hockings, 2010), research at human-primate interfaces has become especially significant over the past decade (Fuentes, 2006; Paterson & Wallis, 2005; Radhakrishna & Sinha, 2011; Riley, 2018). Human-primate interactions are highly diverse in form and frequency, from being neutral and/or involving little or no antagonism (e.g., mutual tolerance, provisioning, religious symbols: Radhakrishna & Sinha, 2011; Sengupta et al., 2015; reviewed in Paterson & Wallis, 2005), to visibly destructive or antagonistic (e.g., destruction of habitat, culling, mutual aggression: Borgerson, 2015; Plumptre et al., 2016; Southwick et al., 1976).

A developing body of research is revealing how anthropogenic factors may impact wildlife social behavior (e.g., cichlid fish, *Neolamprologus pulcher*: Bruintjes & Radford, 2013; Cuban rock iguanas, *Cyclura nubila*: Lacy & Martins, 2003; spotted hyenas, *Crocuta crocuta*: Belton et al., 2018; bottlenose dolphins, *Tursiops truncatus*: Lusseau, 2003). Primates are no exceptions (e.g., agression: Southwick et al., 1976; Ram et al., 2003; affiliation: de la Torre et al., 2000; Marechal et al., 2016; Kaburu et al., 2019a; Marty et al., 2019a). Yet, assessing the

impact of anthropogenic factors on primate affiliative behaviors can be complicated, in part because multiple, sometimes contrasting processes may underlie this impact (Maréchal et al., 2016; Marty et al., 2019a; Pritchard et al., 2014).

One process through which anthropogenic factors may influence primates' affiliative grooming strategies is by influencing animals' time budgets. In group-living animals, time is a valuable but limited resource (Dunbar & Dunbar, 1988; Dunbar et al., 2009; Korstjens & Dunbar, 2007). Many socioecological factors may impose time-constraints on individuals' tendencies to engage in social interactions, e.g. (1) living in large, spatially widespread groups (Berman & Thierry, 2010; Korstjens & Dunbar, 2007; Korstjens et al., 2010), (2) energetic costs associated with lactation or foraging (Altmann, 1974; Dunbar & Dunbar, 1988), and/or (3) increased vigilance when predation risk is high (Creel et al., 2014; reviewed in Dunbar et al., 2009). While primates may navigate such time-constraints by preserving time for more important, beneficial behaviors like social interactions in favor of less beneficial behaviors such as resting (Dunbar & Dunbar, 1988), extreme time-constraints may also impact important behaviors like grooming (Berman & Thierry, 2010; Dunbar, 1992; Lehmann et al., 2007).

Urban landscapes have the potential to impose such extreme constraints, since primates that interact more frequently with humans may also be more vigilant (Kaburu et al., 2019a), or spend more time monitoring human activity in order to access anthropogenic food or to avoid antagonistic interactions with humans (Marty et al., 2019a; Kaburu et al., 2019b). Several studies have shown that primates living in human-impacted areas change their activity budgets (Bryson-Morrison et al., 2017; Jaman & Huffman, 2013; Ruppert et al., 2018; Saj et al., 2001; Singh & Vinathe, 1990), but the impact on inter-individual differences in social behavior remain less clear. More recently, however, our research has revealed how interactions with humans may

127 break up the grooming bout-durations of rhesus macaques (*Macaca mulatta*) (Kaburu et al.,
128 2019a), and reduce the grooming effort (both durations and diversity of partners) of rhesus
129 macaques (Kaburu et al., 2019b) and longtailed macaques (*M. fascicularis*) (Marty et al., 2019a).
130 Life within anthropogenic environments may also expose primates to clumped but
131 predictable patches of food resources of high quality, energy, or digestibility, and thus may have
132 opposite effects on time budgeting relative to grooming (Forthman-Quick, 1988; Mclennan &
133 Ganzhorn, 2017; Riley et al., 2013). If primates are constantly exposed to, and/or prefer
134 consuming human food to natural food, individuals may spend more time foraging on
135 anthropogenic food relative to natural food. Previous studies on primate populations that thrive
136 in anthropogenic landscapes have revealed that such animals also spend more time resting and
137 socializing than populations in less perturbed landscapes, likely due to the high caloric value of
138 anthropogenic foods leading to less time spent consuming or in search of natural food (El Alami
139 et al., 2012; Hockings et al., 2012; Jaman & Huffman, 2013; Koirala et al., 2017; Saj et al., 2001;
140 Thatcher et al., 2019). By the logic of this *free-time* hypothesis, individuals that forage more on
141 anthropogenic food may also have more time (rather than less time, as in time-constraints) or
142 energy to invest in grooming and/or other affiliative interactions (Kaburu et al., 2019b).
143 Here we examine whether interactions with humans influence the time available to invest
144 in social interactions thus impacting inter-individual differences in grooming and other forms of
145 affiliation among semi-urban bonnet macaques (*Macaca radiata*). Bonnet macaques are found in
146 sub-tropical to dry deciduous or scrub-forest environments in Southern India (Siha, 2013), where
147 they also tend to inhabit anthropogenic landscapes (Radhakrishna & Sinha, 2011; Singh & Rao,
148 2004; Sinha & Mukhopadhyay, 2013). Research on other macaque species has revealed that
149 individual attributes like sex and dominance rank may influence variation in animals' tendencies

to interact with humans (rhesus macaques: Beisner et al., 2015; longtailed macaques: Fuentes & Gamerl, 2005) and their grooming strategies (Henzi & Barrett, 1999). In addition, affiliative behaviors may also be impacted by both group-specific attributes (e.g., group size, sex-ratio, home-range size) as these may determine the number and spatial spread of potentially available partners (Berman & Thierry, 2010; Lehmann et al., 2007), and by seasonal differences in climatic conditions which influence ecological factors such as food distribution or human presence/activity and thereby primate socioecology and behavior (Korstjens & Hillyer, 2016). For these reasons, we also accounted for the effects of animal attributes (i.e., sex, dominance rank) and environmental factors (i.e., group ID, season) on macaque grooming and other affiliative interactions.

We tested the following hypotheses and predictions (Figure 1):

H1) *The time-constraints hypothesis:* To determine whether human-macaque interactions impose time-constraints on macaque grooming and other forms of affiliation, we first tested the premise that higher frequency or diversity of interactions with humans is associated with more time spent by macaques monitoring human activity (P1a). In accordance with the time-constraints hypothesis, we then tested whether macaques that monitored human activity more would spend less time grooming (P1b), groom fewer partners (P1c), and engage in lower frequencies of other affiliative interactions (P1d), compared to macaques that monitored less.

H2) *The free-time hypothesis:* To determine whether macaques' interactions with humans were driven by access to anthropogenic food, we first tested the premise that macaques that interacted more with humans also spent more time foraging on anthropogenic food (P2a). In accordance with the free-time hypothesis, we then tested whether increased foraging on anthropogenic food resulted in macaques spending more time grooming (P2b), groom more

partners (P2c), and engage in higher frequencies of other affiliative interactions (P2d), compared to macaques that foraged less on anthropogenic food.

We also examined or controlled for the potential effects of macaques' attributes (specifically sex and dominance rank) and environmental factors (spoecifically group ID and seasonal variation) on monitoring humans, foraging on human foods, and their social behavior. Previous studies on wild bonnet macaques impacted by tourism revealed a sex-biased difference on how human provisioning impacted grooming: provisioning seemed to increase the overall rates of grooming, and grooming reciprocity, among females (Ram et al., 2003; Sinha et al., 2005), but decreased grooming frequency in males (Ram et al., 2003; Sinha et al., 2005). Given this, we also explored whether the effects of macaque monitoring of humans and macaque foraging on anthropogenic food on their grooming and affiliative behaviors was different for different sexes.

Materials and Methods

Study site and subjects

The protocols used in the study were approved by the Institutional Animal Care and Use Committee of the University of California, Davis. These protocols were designed in consultation with the Indian Institute of Science Education and Research Thiruvananthapuram, Kerala, and complied with the legal requirements of India.

We studied two groups of semi-urban bonnet macaques in the Thenmala dam and Ecotourism Recreational Area (8.9^0N, 77^0E) located at the outskirts of the small town of Thenmala within the state of Kerala in Southern India (Figure 2). The Thenmala dam is a reservoir that is located at the border of the Shenduruny Wildlife Sanctuary (8.8^0N, 77.2^0E) and

196 the larger Agasthyamalai Biosphere Reserve (8.6^0N, 77.2^0E). The climate is hot and humid
197 throughout the year, but the area experiences monsoon-based seasonal differences in vegetation
198 and human presence. There is a four-month monsoon season (June – October), followed by a
199 relatively cooler post-monsoon period (November – February), and a hot, relatively drier
200 summer period (March – May). The natural vegetation is primarily composed of dry or moist
201 deciduous trees that are typical of the region. Aside from a few small forest patches, the area is
202 composed of several, continuous anthropogenic landscape features, such as roads, small
203 buildings such as houses, shops and wildlife/ecotourism offices, recreational gardens, and
204 pedestrian pathways/side-walks that lead up to the dam (Figure 2). This environment includes a
205 human population that is composed of both local villagers and shopkeepers, workers at the dam
206 entrance and recreational areas, ecotourism office staff, and tourists from elsewhere who visit the
207 dam and bordering Wildlife and Biosphere Reserves. The density of humans in the area tends to
208 vary across seasons. In particular, tourist influx tends to be highest during the post-monsoon
209 period (four months), and lowest during the hot summer months (three months).

210 The area is home to several groups of bonnet macaques. For our study, we focused on
211 two groups that were somewhat different in size, whose home-ranges overlapped with the
212 anthropogenic landscape features described above, and somewhat overlapped with each other
213 (Figure 2). The study subjects were therefore well-habituated to human presence. The larger
214 group (henceforth LG) comprised 48-58 adults, 26-36 males and 22 females. The smaller group
215 (hereafter SG) comprised 28-30 adults, 10-12 males and 18 females. Barring these fluctuating
216 numbers of males owing to a few individuals that went missing and presumably dispersed during
217 the study and one male in LG dying on account of a road accident, the compositions of the
218 groups remained largely unchanged throughout the course of the study. Aside from a few

exceptional situations in which they disappeared into deep forest cover, both groups were observed throughout most of their range, and within both anthropogenic landscapes and forested areas within their range.

Data Collection

We collected data for a total duration of 11 months spread across all three seasons described above. We used data collection protocols and ethograms that we had previously standardized and implemented on urban-dwelling rhesus macaque in Northern India, and longtailed macaques in Malaysia (Kaburu et al., 2019a, b; Marty et al., 2019a). MA and five field assistants collected data for 2-3 days per week per macaque group, using 10-minute focal animal sampling (Altmann, 1974). The subjects were all adult macaques in both groups. The observers reached inter-observer reliability in focal sampling prior to commencing data collection, with MA as the standard (range of Cohen's Kappa: 0.83 – 0.96). We observed only one macaque group on a given day, and each group twice per week. On each day, we followed a predetermined, randomized sequence to find and sample focal animals. We aimed to obtain two 10-minute focal samples of each animal each week, one in the morning and one in the afternoon. We ended the focal session if an animal went out of sight for > 3 minutes and then conducted a 'make-up' focal session on the same individual at the next available opportunity. Partial focal observations(< 5% of the total number of focal sessions) were ultimately excluded from the analyses.

In each focal session, we recorded all human-macaque and macaque-macaque interactions that involved the focal subject in a continuous manner, capturing both the time of occurrence of each interaction and the sequence. We recorded both more frequently occurring human-macaque interactions such as (i) mutual contact and non-contact aggression, (ii)

avoidance, and (iii) human provisioning of macaques, as well as less frequently occurring interactions initiated by humans towards macaques such as (iv) attention, (v) lure, (vi) taunt, (vii) stare, and (viii) touch (see Kaburu et al., 2019a, b for detailed definitions). Among the macaque-macaque interactions, we recorded (i) agonistic behavior which included contact and non-contact aggression that elicited a clear submissive response from the recipient, (ii) submissive behavior outside of aggressive contexts, and (iii) grooming (including an end-time in addition to the start-time to capture bout-durations) (see Kaburu et al., 2019a, b for detailed definitions). We also recorded other forms of macaque-macaque affiliation, specifically instances of (iv) coalitionary support (an intervention of an on-going conflict to take the side of one of the conflict participants against the other), (v) lip-smacking (rapid, up and down movement of pursed lips), (vi) non-sexual mounting (grabbing the hind-legs of another individual with fore-limbs and briefly rising from the ground to place the fore-limbs on the individual's back), and (vii) silent bare-teeth displays in non-aggressive contexts (hereafter peaceful SBTs). Once every two minutes within each 10-minute focal, we used Point-time Sampling (Altmann, 1974) to record (i) the focal animal's main activity, i.e. whether the animal was resting, grooming, foraging on natural food, foraging on anthropogenic food, in locomotion, or socializing, and (ii) whether or not the animal was monitoring human activity (i.e., looking directly at people: Kaburu et al., 2019a, b; Marty et al., 2019a) All data were entered directly into Samsung tablets (Samsung Tab3/Tab4) using the HanDBase® application (DDH software).

At the end of the 11-month duration, we recorded a total of ~922 hours of observation across 88 focal animals in the two groups, or a mean ± SD of 10.6 ± 3.6 hours of observation per focal animal. We recorded a total of 32,649 instantaneous samples, or a mean ± SD of 325 ± 127 samples per animal.

Behavioral Measures:

Human-macaque interactions: From the focal data on each individual macaque within each season, we calculated its (i) *frequency of human-macaque interactions*, i.e., the number of interactions with humans per hour of observation time. From the instantaneous scan samples, we calculated (ii) the *frequency of monitoring* as the number of scan samples in which a subject was observed monitoring human activity divided by the total number of scan samples on that subject within that season. We also calculated *foraging on anthropogenic food* as the proportion of instantaneous samples in which a subject was observed foraging on human food over the total number of samples in which it was foraging on either natural or human food.

Macaque dominance ranks: From all dyadic agonistic interactions with a clear winner and loser, we calculated the dominance ranks of individuals of each group, using the *Perc* package (Fujii et al., 2015) in R (R Core Team, 2013). Since the biological bases of rank acquisition and function are different for each sex (Bernstein, 1976), we estimated rank orders separately for males (from male-male agonistic interactions) and females (from female-female interactions). In order to control for differences in group size, we standardized the ordinal ranks for each group and sex to create a rank-index, hereafter 'percentile rank', that ranged between 0 (lowest ranked individual) and one (highest ranked individual) (as in Kaburu et al., 2019b; Marty et al., 2019a).

Macaque grooming duration, grooming diversity, and affiliation frequency: From the continuously recorded focal interactions, we calculated, for each individual focal macaque within each season, its (i) *grooming duration* as the amount of time spent either grooming or being groomed by a conspecific, (ii) *grooming diversity* as the total number of individuals with whom the focal individual was engaged in grooming, and (iii) *affiliation frequency* as the number of

instances of engaging in one or more types of short-duration affiliative behaviors (coalitionary supporting, lip-smacking, nonsexual mounting, or peaceful silent bare-teeth displays).

Statistical Analyses:

Some emigrating males were observed for exceptionally short durations of time (<2 months of the 11-month study duration, or < 300 focal minutes). We therefore removed these males, and ran all statistical tests on focal animals that were sampled for a minimum of 300 minutes across 11 months, and within at least two of the three seasons. These criteria yielded a final dataset of 216 behavioral datapoints across 76 macaques (48 in LG (26 males and 22 females) and 28 in SG (10 males and 18 females)) and three seasons, on which we conducted the analyses.

To test all our predictions, we ran Generalized Linear Mixed Models (GLMMs) using the *lme4* package in R (version 3.5.0: R Development Core Team, 2009) (Bates et al., 2015). In each case, we ran either a Negative Binomial model or a Poisson model after verifying whether the model met the criteria for over-dispersion (a Negative Binomial model was chosen) and under-dispersion (a Poisson Model was chosen) respectively. To test the premise for the time-constraints hypothesis, i.e., whether macaques that interacted more with humans also monitored human activity more (H1: P1a), we ran a Negative Binomial model, in which the number of scans in which an individual was observed monitoring humans within each season was the outcome variable. As predictors, we included macaques' frequencies of human-macaque interactions to examine the premise for time-constraints (P1a), as well as sex (categorical variable: male vs female), dominance rank, group ID (categorical variable: LG vs SG), and season of observation (categorical variable: monsoon vs post-monsoon vs summer) to examine their potential effects on monitoring. We set the total number of instantaneous samples on each

macaque within a season as an offset variable and included 'animal ID' (a unique identifier for each individual animal) as a random effect to account for repeated measures across seasons. To test the premise for the free-time hypothesis (H2: P2a), i.e., whether human-macaque interactions positively predicted macaques' tendencies to forage on anthropogenic food, we ran a Poisson model in which the number of scans in which an individual was observed foraging on anthropogenic food was the outcome variable, and included the same set of predictors as above.

To examine whether anthropogenic factors impose time-constraints (i.e., reduced grooming duration, grooming partner diversity, and affiliation frequencies: H1) or free-time (increased grooming duration, partner diversity, or affiliation frequencies: H2) on grooming and affiliative behaviors, we ran nine more GLMMs (summarized in Supplementary Table 1). Specifically, we ran (i) three Negative Binomial models in which the total grooming duration of each focal within each season (in seconds) was the outcome variable (models A1-A3: Supplementary Table 1), (ii) three Poisson models in which the number of grooming partners was the outcome variable (models B1-B3: Supplementary Table 1), and (iii) three Negative Binomial models in which the frequency of other affiliative interactions was the outcome variable (models C1-C3: Supplementary Table 1). In each model, we included, as main effects, macaque monitoring of human activity to test the time-constraints hypothesis (P1b, P1c, P1d), and macaque foraging on anthropogenic food to test the free-time hypothesis (P2b, P2c, P2d). We also included macaques' attributes (i.e., sex and dominance rank) and environmental variables (i.e., group ID and season of observation) to account for their effects on social behavior. To assess potential sex-biased differences on human impact on macaque affiliation, we included an interaction term between sex and monitoring in three models (models A2, B2 and C2), and an interaction between sex and foraging on anthropogenic food in the other three

models (models A3, B3 and C3). In all nine models, we set the total observation time of each macaque within a season as an offset variable and included 'animal ID' as a random effect to account for repeated measures across seasons.

For all GLMMs, we checked model diagnostics related to its validity, stability, and the (lack of) collinearity of model predictors (Cook's distance, DFBetas, DFFits, and Variance Inflation Factors) (Quinn & Keough, 2002; Stevens, 1984). These indicated neither influential cases, nor any deviations from the assumptions of normality and homogeneity of residuals. We also ran Likelihood Ratio Tests (LRTs) using the *lmtest* package in R (Hothorn et al., 2019) to determine whether each GLMM was significantly better-fit than a corresponding 'null' model with no predictors. We only interpreted model coefficients for GLMMs that met this criterion.

Results:

Descriptive Statistics

We recorded a total of 259 human-macaque interactions across 11 months, 96 in the monsoon season, 127 in the post-monsoon season, and 36 in the summer. Of these, the most common interactions were mutual aggression (137 events) and human-to-macaque provisioning (67 events), which together constituted ~79% of all human-macaque interactions. We found significant differences in the frequencies of human-macaque interactions across seasons (monsoon and post-monsoon seasons > summer season: Kruskal-Wallis test: $\chi^2(df = 2) = 22.6, p < 0.01$), and across groups (LG > SG: Kruskal-Wallis rank-sum test: $\chi^2(df = 1) = 13.2, df = 1, p < 0.01$). This further justified our approach to account for these factors while testing our predictions.

Premise for the time-constraints and free-time hypotheses (P1a and P2a):

LRTs revealed that both GLMMs were significantly better-fit than the null model (Table 1). Our GLMM analysis revealed that the frequency of human-macaque interactions had a significant, positive effect on the rates of macaques' monitoring of human activity (Table 1A; Figure 3A). This effect was despite significant effects of macaques' dominance ranks (high ranking individuals monitored more), group ID (members of LG monitored more than those in SG), and observation season (monitoring was highest in the monsoon season, and lowest in the summer), on monitoring (Table 1A). Furthermore, we found that the frequency of human-macaque interactions was positively related to macaques' tendencies to forage on anthropogenic food (Table 1B; Figure 3B). This effect was independent of the significant effects of group ID (LG individuals foraged more than SG individuals), observation season (highest in the post-monsoon and lowest in the summer), and macaques' sex (females foraged more than males), on foraging (Table 1B). These results justify our subsequent analyses testing whether monitoring affects affiliative interactions (time-constraints hypotheses) and whether human-macaque interactions increase macaques' affiliative interactions by increasing macaque access to human food (free-time hypothesis).

Evidence for the time-constraints hypothesis (H1):

We found strong evidence for time-constraints imposed by humans on macaque grooming behavior, but not on other affiliative behaviors. LRTs revealed that all nine GLMMs were significantly better-fit than their corresponding null models (Tables 2-4). GLMMs revealed that macaque monitoring of humans was significantly negatively related to both their grooming duration (P1b; Table 2; Supplementary Table 2; Figure 4) and the diversity of their grooming partners (P1c; Table 3; Supplementary Table 3; Figure 5). These effects were in spite of significant effects of macaques' sex (females groomed more than males), group ID (macaques in

379 LG groomed more than those in SG), and dominance ranks (high ranking individuals groomed
380 for longer, but not necessarily a greater diversity of partners) on grooming effort (Tables 2 and 3;
381 Supplementary Tables 2 and 3). However, monitoring humans had no impact on frequencies of
382 other forms of affiliative behaviors (P1d; Table 4; Supplementary Table 4), which seemed to be
383 more strongly influenced by sex (males showed significantly higher frequencies than females)
384 and observation season (significantly greater in the monsoon compared to the post-monsoon and
385 summer seasons) (Table 4; Supplementary Table 4). Finally, we detected no conditional effect of
386 time-constraints based on sex: interactions between sex and macaque monitoring affected neither
387 grooming (Tables 2 and 3; Supplementary Tables 2 and 3) nor other affiliative behaviors (Table
388 4; Supplementary Table 4).
389 *Evidence for the free-time hypothesis (H2):*
390 We found no evidence for the free-time hypothesis. The GLMMs revealed that macaque
391 foraging on anthropogenic food, either by itself or via interacting with macaques' sex, had no
392 impact on grooming duration (P2b; Table 2), grooming partner diversity (P2c; Table 3), or
393 frequencies of other affiliative interactions (P2d; Table 4).
394
395 **Discussion:**
396 In this study, we examined the impact of anthropogenic factors on grooming and other
397 affiliative interactions among bonnet macaques living in semi-urban landscapes. We found
398 strong evidence for time-constraints: interactions with humans, via influencing primates'
399 tendencies to monitor human activity, seemed to reduce their grooming time and their diversity
400 of grooming partners. On the other hand, macaque foraging on anthropogenic food did not seem
401 to increase their free-time and thereby impact grooming effort or on affiliation frequencies.

Our data established a clear premise for both the time-constraints and the free-time hypotheses: macaques that interacted more frequently with humans showed a greater tendency to monitor human activity, and to forage more on anthropogenic food compared to natural food. Urban primates may monitor humans for many reasons. First, being aware of human activity, behavior, and movement patterns may increase their chances of procuring human foods. Thus, our premise for the time-constraints hypothesis was not mutually exclusive from our premise for the free-time hypothesis: macaques that monitor humans more may also be more successful at procuring or foraging on anthropogenic foods. Nevertheless, such an interdependency of hypotheses was unlikely to be strong for our study-groups, partly because they were exposed to sources of anthropogenic food that were not directly provided to them by humans throughout most of their home-range (e.g., trash, discarded human foods, fruiting trees planted by humans). Such an abundance and ease of access of such anthropogenic food that did not require macaques to directly interact with humans suggests that these macaques may monitor humans for more reasons than just procuring food, for instance to avoid direct conflict (aggression), or because of the potentially unpredictable nature of human-macaque interactions and their outcomes. In semi-urban landscapes (like our study site), the potential benefits of obtaining anthropogenic food from direct interactions with humans is countered by the risk of aggression, injury, or (sometimes) even mortality from humans (Paterson & Wallis, 2005). Bonnet macaques in our study groups indeed experienced a mix of positive (e.g., receiving provisioning) and negative (e.g., aggression, mortality from car accidents) interactions with humans, which may explain why macaques that monitored human activity more also interacted more frequently with humans.

In support of the time-constraints hypothesis, monitoring humans seemed to lower macaques' grooming effort, a result that was generally consistent with our other recent findings

425 on urban-dwelling rhesus and longtailed macaques (Kaburu et al., 2019b; Marty et al., 2019a).
426 When socioecological factors like group sizes or resource distribution impose time-constraints
427 on primates' grooming, animals may adjust their strategies by lowering either per capita
428 grooming effort or by reducing the number of grooming partners, but rarely both (Berman &
429 Thierry, 2010; Dunbar & Dunbar, 1988; Dunbar et al., 2009; Lehmann et al., 2007). With
430 regards to the time-constraints imposed by anthropogenic factors, bonnet macaques showed a
431 reduction in both grooming time and partner diversity, which was in contrast to our findings on
432 longtailed macaques in which monitoring reduced grooming duration but not partner diversity
433 (Marty et al., 2019a). Nonetheless, we speculate that the magnitudes of these effects for bonnet
434 macaques may be smaller than those that we detected for longtailed macaques and rhesus
435 macaques, given potential species-typical differences in social behavior (Thierry, 2007), or
436 (more likely) the markedly lower overall human impact on the macaques in Thenmala compared
437 to the populations we studied in Northern India and Malaysia (McCowan, *Unpublished Data*).
438 Confirming this awaits comparative analyses across species/sites.
439 Unlike grooming, monitoring humans did not seem to impose time-constraints on other
440 forms of affiliation. One primary reason for this could be that these behaviors occur less
441 frequently and are brief in duration. In macaque societies, giving and receiving coalitionary
442 support is critical to the maintenance or ascendancy of male dominance status, and the
443 maintenance of strong alliances between close kin and friends (van Hooff & van Schaik, 1992).
444 Furthermore, affiliative signaling behaviors such as lip-smacking and silent bare-teeth displays in
445 non-aggressive contexts, in addition to grooming, may also function to establish and maintain
446 strong social bonds (Silk et al., 2003; Young et al., 2014). Retaining such short-duration
447 affiliative behaviors may also be especially important among primate groups living in human-

448 impacted landscapes, both to maintain their social bonds while compromising on their grooming
449 time and effort, and to deal with the stressful conditions that such environments may present
450 (Marechal et al., 2016).

451 We found no evidence for the free-time hypothesis - macaque foraging on anthropogenic
452 food had no impact on their grooming behavior. This was consistent with our previous findings
453 on rhesus macaques in Northern India (Kaburu et al., 2019b), but inconsistent with many
454 previous studies that revealed that primates that are more exposed to human-provisioned food
455 sources spend more (rather than less) time resting or socializing compared to those less exposed
456 to anthropogenic factors. The free-time hypothesis is based on the pretext that anthropogenic
457 foods are more abundant, spatiotemporally predictable, and have higher calorific value than
458 natural foods of primates (Mclennan & Ganzhorn, 2017; Oro & Genovart, 2013; Riley et al.,
459 2013; Saj et al., 1999). This may be true for primate populations that are professionally
460 provisioned (Marty et al., 2019b), i.e. experience regular human provisioning that is
461 spatiotemporally predictable, i.e., occurs at specific times and/or at specific locations (e.g., El
462 Alami et al., 2012; Hockings et al., 2012; Jaman & Huffman, 2013; Koirala et al., 2017; Saj et
463 al., 2001; Thatcher et al., 2019). At our study site, however, provisioning occurred at random
464 times and areas within the macaques' home range (i.e., was spatiotemporally unpredictable:
465 Marty et al., 2019b). Such unpredictability could mean that these macaques may incur energetic
466 costs in procuring anthropogenic foods.

467 There was not an effect of subjects' sex on the impact of anthropogenic factors on
468 macaque grooming or other forms of affiliation. This was in contrast to previous work on wild
469 but occasionally provisioned bonnet macaques, which revealed that human provisioning seemed
470 to increase grooming frequency and reciprocity among females (Ram et al., 2003), but not so in

males which showed a decrease in grooming frequency (Sinha et al., 2005). We speculate that urban environments can support bonnet macaque groups that may be generally larger in size, show more even sex ratios, lower within-group competition, and greater within-group social tolerance among both males and females, in comparison to macaque groups living in forested environments that experience little/minimal human impact. The latter may show the opposite characteristics and, in extreme socioecological conditions, intense male-male competition and uni-male social organizations (Sinha et al., 2005). Consequently, both males and females in urban bonnet macaque groups (like ours) may maintain generally strong grooming relationships, although, as our results show, individuals subject to anthropogenic time-constraints seem to uniformly, independent of their sex, forego some grooming effort.

Given that grooming and other affiliative interactions can be strongly influenced by many socioecological or environmental factors, it is noteworthy that our findings were independent of the effects of macaque group ID, dominance rank, sex, and seasonal variation (which likely impacted the distribution and abundance of resources), which seemed to impact grooming and/or other forms of affiliation to varying extents. Predation pressure was relatively low or absent in the area. For these reasons, we remain confident that anthropogenic factors indeed negatively impacted bonnet macaque grooming behavior, and had no impact on other forms of affiliation. Although we focused on overall frequencies of human-macaque interactions and monitoring of humans, it is conceivable that specific types or sequences of interactions that are especially time-consuming were more likely than others to impose time-constraints on grooming (Kaburu et al., 2019b). This awaits research. Furthermore, whether such reductions in grooming effort also impact changes to the structure of macaques' grooming social networks also awaits investigation.

In conclusion, our study reveals how interactions with humans constrains the time available for bonnet macaques to engage in social grooming behavior. These results add to a growing, fundamentally important body of research related to how humans and anthropogenic factors may impact the behavior of wildlife, and free-living primates in particular. Since grooming may strongly impact primate health and fitness outcomes (Kappeler et al., 2015; Nunn et al., 2015), our findings that anthropogenic factors lead to a reduction in macaques' grooming effort have indirect implications for the conservation of bonnet macaques. Although listed as a 'Least Concern' species by the IUCN (Singh et al., 2008; Singh & Rao, 2004), bonnet macaques are not as geographically widespread as other primate species such as rhesus and longtailed macaques, and remain Red-Listed primates with a decreasing population trend (Radhakrishna & Sinha, 2011; Singh & Rao, 2004; Sinha, 2013; Sinha & Mukhopadhyay, 2013). Thus, future work on this species, and on other vulnerable or endangered primates that overlap with anthropogenic landscapes, should also focus on whether/how changes to the social behavioral strategies of individual primates that are impacted by humans may impact indicators of their health and fitness.

Acknowledgements:

We thank the Kerala Forest Department and the Indian Institute of Science Education and Research (IISER) Thiruvananthapuram for facilitating our research in Thenmala. We thank Dr. Hema Somanathan and her research group at IISER Thiruvananthapuram for providing access to their Field Station, and for assisting with logistics related to the commencement of fieldwork in Thenmala. We are grateful to Pooja Dongre, Mohammed Ismail, Megha Majoe, Rajarshi Saha, Alvaro Sobrino, and Menno Van Berkel for their assistance with data collection. We are grateful

to two anonymous reviewers whose comments have helped improved the quality of the manuscript. This work was supported by the American National Science Foundation Coupled Natural and Human Systems grant (NSF-CNH #1518555) awarded to the PI Dr. Brenda McCowan.

Literature Cited:

Altmann, J. (1974). Observational study of Behavior: sampling methods. *Behaviour*, *49*, 227–267.

Altmann, S. A. (1974). Baboons, space, time, and energy. *American Zoologist*, *248*, 221–248.

Barrett, L., Gaynor, D., & Henzi, S. P. (2002). A dynamic interaction between aggression and grooming reciprocity among female chacma baboons, 1047–1053. https://doi.org/10.1006/anbe.2002.3008

Barua, M., Bhagwat, S. A., & Jadhav, S. (2013). The hidden dimensions of human – wildlife conflict: Health impacts, opportunity and transaction costs. *Biological Conservation*, *157*, 309–316.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed Effects Models Using lme4. Journal of Statistical Software, 67, 1-48.

Beisner, B. A., Heagerty, A., Seil, S. K., Balasubramaniam, K. N., Atwill, E. R., Gupta, B. K., … McCowan, B. (2015). Human-wildlife conflict: Proximate predictors of aggression between humans and rhesus macaques in India. *American Journal of Physical Anthropology*, *156*(2), 286–294. https://doi.org/10.1002/ajpa.22649

Belton, L. E., Cameron, E. Z., & Dalerum, F. (2018). Social networks of spotted hyaenas in areas of contrasting human activity and infrastructure. *Animal Behaviour*, *135*, 13–23.

https://doi.org/10.1016/j.anbehav.2017.10.027

Berman, C. M., & Thierry, B. (2010). Variation in kin bias: species differences and time-constraints in macaques. *Behaviour*, *147*, 1863–1887. https://doi.org/10.1163/000579510X539691

Bernstein, I. S. (1976). Dominance, aggression and reproduction in primate societies. *Journal of Theoretical Biology*, *60*(2), 459–472. https://doi.org/10.1016/0022-5193(76)90072-2

Borgerson, C. (2015). The effects of illegal hunting and habitat on two sympatric endangered primates, 74–93. https://doi.org/10.1007/s10764-015-9812-x

Bruintjes, R., & Radford, A. N. (2013). Context-dependent impacts of anthropogenic noise on individual and social behaviour in a cooperatively breeding fish. *Animal Behaviour*, *85*(6), 1343–1349. https://doi.org/10.1016/j.anbehav.2013.03.025

Bryson-Morrison, N., Tzanopoulos, J., Matsuzawa, T., & Humle, T. (2017). Activity and habitat use of chimpanzees (*Pan troglodytes verus*) in the anthropogenic landscape of Bossou, Guinea, West Africa. *International Journal of Primatology*, *38*(2), 282–302. https://doi.org/10.1007/s10764-016-9947-4

Chapais, B. (2005). Kinship, competence and cooperation in primates. In P. M. Kappeler & C. P. Van Schaik (Eds.), *Cooperation in Primates and Humans: Mechanisms and Evolution* (pp. 47–64). Cambridge: Cambridge University Press.

Cords, M. (2019). Predator vigilance costs of allogrooming in wild blue monkeys. *Behaviour*, *132*(7), 559–569.

Creel, S., Schuette, P., & Christianson, D. (2014). Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community, *25*, 773–784. https://doi.org/10.1093/beheco/aru050

de la Torre, S., Snowdon, C. T., & Bejarano, M. (2000). Effects of human activities on wild pygmy marmosets in Ecuadorian Amazonia. *Biological Conservation*, *94*(2), 153-163.

Dickman, A. J. (2010). Complexities of conflict: The importance of considering social factors for effectively resolving human-wildlife conflict. *Animal Conservation*, *13*(5), 458–466. https://doi.org/10.1111/j.1469-1795.2010.00368.x

Duboscq, J., Romano, V., Sueur, C., & Macintosh, A. J. J. (2016). Network centrality and seasonality interact to predict lice load in a social primate. *Scientific Reports*, *6*(April 2015), 1–13. https://doi.org/10.1038/srep22095

Dunbar, R. I. M. (1992). Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology*, *31*, 35–49. https://doi.org/10.1007/BF00167814

Dunbar, R. I. M., & Dunbar, P. (1988). Maternal time budgets of gelada baboons. *Animal Behaviour*, *36*(4), 970–980. https://doi.org/10.1016/S0003-3472(88)80055-1

Dunbar, R. I. M., Korstjens, A. H., & Lehmann, J. (2009). Time as an ecological constraint. *Biological Reviews*, *84*(3), 413–429. https://doi.org/10.1111/j.1469-185X.2009.00080.x

El Alami, A., Lavieren, E., Rachida, A., & Chait, A. (2012). Differences in activity budgets and diet between semiprovisioned and wild-feeding groups of the endangered Barbary macaque (*Macaca sylvanus*) in the central high Atlas Mountains, Morocco. *American Journal of Primatology*, *74*, 210–216. https://doi.org/10.1002/ajp.21989

Forthman-Quick, D. (1988). Dynamics of exploitation: differential energetic adaptations of two troops of baboons to recent human contact. In J. E. Fa & C. H. Southwick (Eds.), *Ecology and behavior of food enhanced primate groups* (pp. 25–51). New York: Liss.

Fuentes, A. (2006). Human-nonhuman primate interconnections and their relevance to Anthropology. *Ecological and Environmental Anthropology*, *2*(2), 1–11. Retrieved from

http://digitalcommons.unl.edu/icwdmeea%5Cnhttp://digitalcommons.unl.edu/icwdmeea/1

Fuentes, A., & Gamerl, S. (2005). Disproportionate participation by age/sex classes in aggressive interactions between long-tailed macaques (*Macaca fascicularis*) and human tourists at Padangtegal monkey forest, Bali, Indonesia. *American Journal of Primatology*, *66*(2), 197–204. https://doi.org/10.1002/ajp.20138

Fuentes, A., & Hockings, K. J. (2010). The ethnoprimatological approach in primatology. *American Journal of Primatology*, *72*(10), 841–847. https://doi.org/10.1002/ajp.20844

Fujii, K., Jin, J., Shev, A., Beisner, B., McCowan, B., & Fushing, H. (2015). *Perc: using percolation and conductance to find information flow certainty in a direct network*. R Package Version 0.1.

Hemelrijk, C. K. (1999). An individual-orientated model of the emergence of despotic and egalitarian societies. *Proceedings of the Royal Society B*, *266*, 361–369.

Henzi, S. P., & Barrett, L. (1999). The value of grooming to female primates. *Primates*, *40*, 47–59. Retrieved from http://www.springerlink.com/index/W70127G802273205.pdf

Hinde, R. A. (1976). Interactions, relationships and social structure. *Man*, *11*(1), 1–17.

Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2012). Socioecological adaptations by chimpanzees, *Pan troglodytes verus*, inhabiting an anthropogenically impacted habitat. *Animal Behaviour*, *83*(3), 801–810. https://doi.org/10.1016/j.anbehav.2012.01.002

Hothorn, T., Zeileis, A., Farebrother, R. W., Cummins, C., Millo, G., & Mitchell, D. (2019). Lmtest: testing linear regression models (R Package Version 3.3.0) https://CRAN.R-project.org/package=lmtest

Jaman, M. F., & Huffman, M. A. (2013). The effect of urban and rural habitats and resource type on activity budgets of commensal rhesus macaques (*Macaca mulatta*) in Bangladesh.

Primates, *54*(1), 49–59. https://doi.org/10.1007/s10329-012-0330-6.

Kaburu, S. S. K., Marty, P. R., Beisner, B., Balasubramaniam, K. N., Bliss-Moreau, E., Kaur, K., … McCowan, B. (2019a). Rates of human–macaque interactions affect grooming behavior among urban-dwelling rhesus macaques (*Macaca mulatta*). *American Journal of Physical Anthropology*, *168*(1), 92–103. https://doi.org/10.1002/ajpa.23722

Kaburu, S. S. K., Beisner, B. A., Balasubramaniam, K. N., Marty, P. R., Bliss-Moreau, E., Mohan, L., … McCowan, B. (2019b). Interactions with humans impose time-constraints on commensal rhesus macaques (*Macaca mulatta*). *Behaviour, In Press*.

Kappeler, P. M., Cremer, S., & Nunn, C. L. (2015). Sociality and health: Impacts of sociality on disease susceptibility and transmission in animal and human societies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370, 20140116. https://doi.org/10.1098/rstb.2014.0116

Kappeler, P. M., & Van Schaik, C. P. (2002). Evolution of primate social systems. *International Journal of Primatology*, *23*(4), 707–740. https://doi.org/10.1023/A

Kasper, C., & Voelkl, Æ. B. (2009). A social network analysis of primate groups. *Primates*, *50*, 343–356. https://doi.org/10.1007/s10329-009-0153-2

Keverne, E. B., Artensz, N. D. I., & Tute, B. (1989). Beta-Endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology*, *14*(l), 155–161.

Koirala, S., Chalise, M., Katuwal, H. B., Gaire, R., Pandey, B., & Ogawa, H. (2017). Diet and activity of *Macaca assamensis* in wild and semi-provisioned groups in Shivapuri Nagarjun National Park, Nepal. *Folia Primatologica*, *88*, 57–74. https://doi.org/10.1159/000477581

Korstjens, A. H., & Dunbar, R. I. M. (2007). Time-constraints limit group sizes and distribution

in red and black-and-white Colobus. *International Journal of Primatology*, *28*(3), 551–575. https://doi.org/10.1007/s10764-007-9148-2

Korstjens, A. H., & Hillyer, A. P. (2016). Primates and climate change: A review of current knowledge. In S. A. Wich, & A. J. Marshall (Eds.), An introduction to primate conservation (pp. 175–192). Oxford: Oxford University Press

Korstjens, A. H., Lehmann, J., & Dunbar, R. I. M. (2010). Resting time as an ecological constraint on primate biogeography. *Animal Behaviour*, *79*(2), 361–374. https://doi.org/10.1016/j.anbehav.2009.11.012

Lacy, K. E., & Martins, E. P. (2003). The effect of anthropogenic habitat usage on the social behaviour of a vulnerable species, *Cyclura nubila*, 3–9. https://doi.org/10.1017/S1367943003003020

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Group size, grooming and social cohesion in primates. *Animal Behaviour*, *74*(6), 1617–1629. https://doi.org/10.1016/j.anbehav.2006.10.025

Lusseau, D. (2003). Effects of tour boats on the behavior of bottlenose dolphins: using markov chains to model anthropogenic impacts. *Conservation Biology*, *17*(6), 1785–1793.

Maréchal, L., MacLarnon, A., Majolo, B., & Semple, S. (2016). Primates' behavioural responses to tourists: Evidence for a trade-off between potential risks and benefits. *Scientific Reports*, *6*(June), 1–11. https://doi.org/10.1038/srep32465

Marty, P. R., Beisner, B., Kaburu, S. S. K., Balasubramaniam, K., Bliss-Moreau, E., Ruppert, N., … McCowan, B. (2019a). Time-constraints imposed by anthropogenic environments alter social behaviour in long-tailed macaques. *Animal Behaviour*, *150*, 157–165. https://doi.org/10.1016/j.anbehav.2019.02.010

Marty, P. R., Balasubramaniam, K. N., Kaburu, S. S. K., Hubbard, J., Beisner, B. A., Bliss-Moreau, E., Arlet, M., Ruppert, N., Arlet, M. E., Sah, S. A. M., Ismail, A., Mohan, L., Rattan, S. K., Kodandaramaiah, U., & McCowan, B. (2019b). Individuals in urban dwelling primate species face unequal benefits associated with living in an anthropogenic environment. *Primates*, Published Online: https://doi.org/10.1007/s10329-019-00775-4

McFarland, R., Henzi, P. S., Barrett, L., Wanigaratne, A., Coetzee, E., Fuller, A., Hetem, R. S., Mitchell, D., & Maloney, S. K. (2016). Thermal consequences of increased pelt loft infer an additional utilitarian function for grooming. *American Journal of Primatology*, 78, 456-461.

McFarland, R. (2018). Grooming. In M. Bezanson, K. C. MacKinnon, E. Riley, C. J. Campbell, K. A. I. Nekaris, A. Estrada, … A. Fuentes (Eds.), *The International Encyclopedia of Primatology*. John Wiley & Sons, Inc.

Mclennan, M. R., & Ganzhorn, J. U. (2017). Nutritional characteristics of wild and cultivated foods for chimpanzees (*Pan troglodytes*) in agricultural landscapes. *International Journal of Primatology, 38*, 122–150. https://doi.org/10.1007/s10764-016-9940-y

Nunn, C. L. (2012). Primate disease ecology in comparative and theoretical perspective. *American Journal of Primatology, 74*(6), 497–509. https://doi.org/10.1002/ajp.21986

Nunn, C. L., Craft, M. E., Gillespie, T. R., Schaller, M., & Kappeler, P. M. (2015). The sociality–health–fitness nexus: synthesis, conclusions and future directions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1669), 20140115.

Nyhus, P. J. (2016). Human–Wildlife Conflict and Coexistence. *Ann. Rev. Environ. Resour., 41*, 143-171. https://doi.org/10.1146/annurev-environ-110615-085634

Oro, D., & Genovart, M. (2013). Ecological and evolutionary implications of food subsidies

678 from humans. *Ecology Letters*, *16*, 1501–1514. https://doi.org/10.1111/ele.12187
679 Pasquaretta, C., Leve, M., Claidiere, N., van de Waal, E., Whiten, A., MacIntosh, A. J. J., …
680 Sueur, C. (2014). Social networks in primates: smart and tolerant species have more
681 efficient networks. *Scientific Reports*, *4*(1), 1–8. https://doi.org/10.1038/srep07600
682 Paterson, J. D., & Wallis, J. (2005). *Commensalism and Conflict: the Human–Primate Interface*.
683 Norman, Oklahoma: American Society of Primatologists.
684 Plumptre, A. J., Nixon, S., Kujirakwinja, D. K., Vieilledent, G., Critchlow, R., Williamson, E.
685 A., … Hall, S. (2016). Catastrophic decline of world's largest primate: 80 % Loss of
686 Grauer's gorilla (*Gorilla beringei graueri*) population justifies critically endangered status,
687 1–13. https://doi.org/10.1371/journal.pone.0162697
688 Pritchard, A. J., Sheeran, L. K., Gabriel, K. I., Li, J., & Wagner, R. S. (2014). Behaviors that
689 predict personality components in adult free-ranging Tibetan macaques *Macaca thibetana*.
690 *Current Zoology*, *60*, 362–372.
691 Puga-gonzalez, I., & Sueur, C. (2017). Emergence of complex social networks from spatial
692 structure and rules of thumb: a modelling approach. *Ecological Complexity*, *31*, 189–200.
693 https://doi.org/10.1016/j.ecocom.2017.07.004
694 Quinn, G. P., & Keough, M. J. (2002). *Experimental Designs and Data Analysis for Biologists*.
695 Cambridge: Cambridge University Press
696 R Core Team (2013). R: A Language and Environment for Statistical Computing. R Foundation
697 for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/
698 Radhakrishna, S., & Sinha, A. (2011). Less than wild? Commensal primates and wildlife
699 conservation. *Journal of Biosciences*, *36*(5), 749–753. https://doi.org/10.1007/s12038-011-
700 9145-7

Ram, S., Venkatachalam, S., & Sinha, A. (2003). Changing social strategies of wild female bonnet macaques during natural foraging and on provisioning. *Current Science*, *84*(6), 780–790.

Riley, E. P. (2018). The Maturation of ethnoprimatology: theoretical and methodological pluralism. *International Journal of Primatology*, *39*(5), 705–729. https://doi.org/10.1007/s10764-018-0064-4

Riley, E. P., & Priston, N. E. C. (2010). Macaques in farms and folklore: exploring the human-nonhuman primate interface in Sulawesi, Indonesia. *American Journal of Primatology*, *72*(10), 848–854. https://doi.org/10.1002/ajp.20798

Riley, E. P., Tolbert, B., & Farida, W. R. (2013). Nutritional content explains the attractiveness of cacao to crop raiding Tonkean macaques. *Current Zoology*, *59*(2), 160–169.

Ruppert, N., Holzner, A., See, K. W., Gisbrecht, A., & Beck, A. (2018). Activity budgets and habitat use of wild southern pig-tailed macaques (*Macaca nemestrina*) in Oil Palm Plantation and Forest. *International Journal of Primatology*, *39*, 237–251.

Saj, T. L., Sicotte, P., & Paterson, J. D. (1999). Influence of human food consumption on the time budget of vervets. *International Journal of Primatology*, *20*(6), 977–994.

Saj, T. L., Sicotte, P., & Paterson, J. D. (2001). The conflict between vervet monkeys and farmers at the forest edge in Entebbe, Uganda. *African Journal of Ecology*, *39*, 195–199.

Schino, G. (2001). Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour*, *62*, 265–271. https://doi.org/10.1006/anbe.2001.1750

Sengupta, A., McConkey, K. R., & Radhakrishna, S. (2015). Primates, provisioning and plants: Impacts of human cultural behaviours on primateecological functions. *PLoS ONE*, *10*(11), 1–13. https://doi.org/10.1371/journal.pone.0140961

724 Seyfarth, R. M. (1977). A model of social grooming among adult female primates. *Journal of*
725 *Theoretical Biology*, *65*, 671–698.
726 Shutt, K., Maclarnon, A., Heistermann, M., & Semple, S. (2007). Grooming in Barbary
727 macaques: better to give than to receive? *Biology Letters*, *3*(January), 231–233.
728 https://doi.org/10.1098/rsbl.2007.0052
729 Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant
730 survival. *Science*, 302, 1231e1234.
731 Singh, M., Kumar, A., & Molur, S. (2008). *Macaca radiata*, Bonnet Macaque. *The IUCN List of*
732 *Threatened Species*, *ISSN 2307*-.
733 Singh, M., & Rao, N. R. (2004). Population Dynamics and Conservation of Commensal Bonnet
734 Macaques. *International Journal of Primatology*, *25*(4), 847–859.
735 Singh, M., & Vinathe, S. (1990). Inter-population Differences in the Time Budgets of Bonnet
736 Monkeys (Macaca radiata). *Primates*, *31*, 589–596.
737 Sinha, A. (2013). Bonnet Macaque *Macaca radiata*. In A. J. T. Johnsingh & N. Manjrekar
738 (Eds.), *Mammals of South Asia Volume One* (pp. 148–169). Hyderabad: Universities Press.
739 Sinha, A., & Mukhopadhyay, K. (2013). The Monkey in the Town's Commons, Revisited: An
740 Anthropogenic History of the Indian Bonnet Macaque. In S. Radhakrishna, M. A. Huffman,
741 & A. Sinha (Eds.), *The Macaque Connection: Cooperation and Conflict between Humans*
742 *and Macaques* (pp. 187–208). New York: Springer-Verlag. https://doi.org/10.1007/978-1-
743 4614-3967-7
744 Sinha, A., Mukhopadhyay, K., Datta-Roy, A., & Ram, S. (2005). Ecology proposes, behaviour
745 disposes: Ecological variability in social organization and male behavioural strategies
746 among wild bonnet macaques. *Current Science*, *89*(7), 1166–1179.

https://doi.org/10.2307/24110968

Southwick, C. H., Siddioi, M. F., Farooqui, M. Y., & Pal, B. C. (1976). Effects of artificial feeding on aggressive behaviour of rhesus monkeys in India. *Animal Behaviour*, *24*(1), 11–15. https://doi.org/10.1016/S0003-3472(76)80093-0

Sterck, E. H. M., Watts, D. P., & Van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates, 291–309.

Stevens, J. P. (1984). Outliers and influential data points in regression analysis. *Quantitative Methods in Psychology*, *95*, 334–344.

Tanaka, J., & Takefushi, H. (1993). Elimination of external parasites (lice) is the primary function of grooming in free-ranging Japanese macaques. *Anthropol. Sci.*, *101*(2), 187–193.

Thatcher, H. R., Downs, C. T., & Koyama, N. F. (2019). Landscape and Urban Planning Anthropogenic influences on the time budgets of urban vervet monkeys. *Landscape and Urban Planning*, *181*, 38–44. https://doi.org/10.1016/j.landurbplan.2018.09.014

Thierry, B. (2007). Unity in diversity: Lessons from macaque societies. *Evolutionary Anthropology*, *16*(6), 224–238. https://doi.org/10.1002/evan.20147

van Hooff, J. A. R. A. M., & van Schaik, C. P. (1992). Cooperation in competition: The ecology of primate bonds. In Harcourt, A. H., and de Waal, F. B. M. (eds.), Coalitions and Alliances in Humans and Other Animals, Oxford University Press, Oxford, pp. 357–389

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, *75*(3), 262–300.

Young, C., Majolo, B., Heistermann, M., Schülke, O., & Ostner, J. (2014). Responses to social and environmental stress are attenuated by strong male bonds in wild macaques.

Proceedings of the National Academy of Sciences, *111*(51), 18195–18200. https://doi.org/10.1073/pnas.1411450111.

Figure Legends:

Figure 1 The time-constraints and free-time hypotheses tested in this study. Bold arrows indicate the overall predicted directions (increase versus decrease) of variation in grooming duration, diversity, and other affiliative interactions based on each hypothesis.

Figure 2 Map of the study site, i.e., the Thenmala Dam and Ecotourism Recreational Area in Kerala, Southern India (8.9^0N, 77^0E). We collected data on two groups of bonnet macaques (*Macaca radiata*) in the area. Grey areas that are not represented in the key above indicate natural or forested landscape features.

Figure 3 Relationship between the frequency of human-macaque interactions and model-predicted rates of (A) macaque monitoring of human activity (H1: P1a) and (B) foraging on anthropogenic food (H2: P2a). Y axis values were calculated by dividing the model-predicted values (of monitoring and foraging on anthropogenic food) by the total number of scans set as an offset variable in each model.

Figure 4 Relationship between macaque monitoring of human activity and grooming duration (model-predicted outcome from model A1: H1: P1b). Y axis values represent model-predicted proportions of time spent grooming, calculated by dividing the model-predicted values of grooming duration by macaque observation times set as an offset variable in the model.

Figure 5 Relationship between macaque monitoring of human activity and grooming partner diversity (model-predicted outcome from model B1: H1: P1c). Y axis values represent model-predicted numbers of grooming partners per unit time, calculated by dividing the model-

predicted values of grooming partner diversity by macaque observation times set as an offset variable in the model.